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An analysis of the learning process underlying filial imprinting

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SUMMARY

Filial imprinting is the process through which a young animal comes to restrict its social behaviour to a particular object or class of objects, usually its mother and siblings. Even though the first detailed description dates from over 50 years ago (Lorenz, 1935), the exact nature of the learning process underlying filial imprinting is still unclear. The present study deals with this problem, and the approach taken is to inquire whether the learning process underlying in filial imprinting is similar to that involved in associative learning. Associative learning is the process through which animals learn about relations among events, and a well-known example is Pavlovian conditioning. Several investigators have claimed that filial imprinting is a form of associative learning, as opposed to perceptual learning, which does not involve an association with reinforcement. To investigate this issue, the present study examined whether the outcome of experiments on filial imprinting can be adequately predicted or explained by associative-learning theory. The subjects of the study were junglefowl chicks (*Gallus gallus spadiceus*; chapters 2-6) and domestic chicks (*Gallus gallus domesticus*; chapter 7), and the objects were artificial.

When chicks were exposed to a novel imprinting object in the presence of the familiar object (chapter 2), imprinting on the novel object was impaired when the objects were relatively far apart. When the objects were placed against each other, imprinting on the novel object was not impaired, and when the objects were only slightly apart, imprinting was slightly impaired in one of the experimental groups, but not in the other. When chicks were exposed to two objects simultaneously (chapter 3), which were relatively far apart, they became strongly attached to only one of them, either the one or the other. But when the objects were interlocked, chicks became strongly attached to each object, and when the objects were slightly apart, development of attachment to each object was retarded.

It is proposed that when objects are relatively far apart, chicks do not receive equal exposure to each of them during the motivational state in which imprinting may occur. When a chick is not motivated to seek contact with an imprinting object, it may become familiar with other objects, which, however, do not acquire control over filial behaviour. Indeed, the non-preferred of two objects to which chicks had been exposed simultaneously (chapter 4) did not acquire control over filial behaviour, and subsequent imprinting to it was retarded. In chapter 5 it was suggested that when chicks are motivated to seek contact with the imprinting object they will flee to the location where they last saw it, which ensures rapid establishment of contact. This position response contributes to the chicks not attending to other objects during the motivational state to imprint. Knowledge about the location of the imprinting object seems to be stored in a labile form of memory, and is probably not included in the

internal representation of the object.

When objects are more closely together, chicks attend to both of them during the motivational state to imprint, and it is proposed that processes operating at the level of the acquisition of control over filial behaviour by internal representations of objects may then follow the rules of associative learning. Differences between the situations with the objects slightly apart and the objects placed against each other or interlocked, can be explained at the level of the formation of internal representations.

With respect to the interaction between learning about colour and shape (chapter 5) and one colour of an object and another (chapter 6), it was shown that attachment to one feature is stronger the more effective the other feature is. Also, auditory learning was enhanced by visual stimulation, and *vice versa* (chapter 7). These results can be explained by assuming that features do not only become associated with reinforcement, but also with each other, and, more importantly, that reinforcement is stronger when an object is a more effective imprinting stimulus.

Taken together, it was concluded that applying associative-learning theory to the case of filial imprinting did not generate accurate predictions, but that it is still possible to explain the results within an associative-learning framework (section 8.1). However, the results do not necessarily contradict a perceptual-learning theory, and therefore a quest for the US in imprinting was conducted (section 8.2). At a behavioural level there are close similarities between the US in filial imprinting and reinforcement involved in brain-stimulation reward, and evidence at the physiological level reveals that both are related to the brain catecholamine system, which is involved in arousal and sensitivity to stress. It was argued that the learning rules involved in connecting the representation of an object to the executive system of filial imprinting are similar to those involved in associative learning, since this system is active while the representation is stored in memory (section 8.3). Thus, although the distinction between associative and perceptual learning has diminished over the past years due to advancing insights on the nature of these processes, filial imprinting can be best conceptualized as a form of associative learning. Finally, a more general description of the initial stages of the development of filial attachments is presented, incorporating the present conclusions and speculations.